# DARWIN'S TYPE SPECIMENS OF VARIETIES OF *BALANUS AMPHITRITE*



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*Pp. 271–296 ; Plates 1–10; 1 Text-figure*

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# DARWIN'S TYPE SPECIMENS OF VARIETIES OF *BALANUS AMPHITRITE*

*By* J. P. HARDING

Darwin (1854), p. 197, and again on p. 242 vividly describes the great variability of *Balanus amphitrite* and *B. tintinnabulum* and the difficulty he had in coming to the decision as to whether the various varieties he established for these two species should be regarded as varieties or as separate species. *Balanus amphitrite* like *B. tintinnabulum* is frequently found attached to ships and much of the extreme tendency to vary may well, as Darwin himself suggested, be due to their frequently being transported to new localities. Since Darwin's time, many workers have been faced with the same problem and are hampered by the fact that Darwin was unable to publish many illustrations and that his descriptions of the animal parts of the varieties are inadequate by present standards more than a century later. It is now forty-five years since Pilsbry (1916, pp. 93–94) wrote, " The definition of the sub-species of *Balanus amphitrite* is a very intricate problem . . . first of all the Darwin collection must be restudied and type localities for his varieties selected". The purpose of this paper is to publish the results of such a study. Much of the material studied by Darwin no longer exists ; but there is a cabinet of dry shells mounted on slabs in the British Museum. In the account which follows these specimens are referred to the slab to which they were attached, e.g. Slab 17.1.22. There are also a number of microscopic slides of mouth-parts and other appendages dissected by Darwin now in the University Museum of Zoology, Cambridge ; these are referred to by reference numbers used in the catalogue at Cambridge and written on the slide, e.g. Cambridge Slide 151. In addition Darwin prepared a series of dry specimens of the various varieties of *Balanus amphitrite* for the British Museum and for many years these have been on public exhibition mounted on slabs with two lists of the specimens in Darwin's handwriting alongside ; one list is of " Shells " and the other of " Opercular Valves ", and these will be referred to by the number used in Darwin's lists, e.g. Shell 28, Opercular Valve 4. It was anticipated that the most useful material for the present purposes would be on these slabs but they have proved disappointing. The lists correspond with the specimens only approximately, a number of specimens are now missing and others have evidently been substituted at some time by other material.

Darwin describes nine varieties or sub-species of *Balanus amphitrite* and for most of these I have been able to find and select as lectotype, a specimen complete with opercular valves and animal parts which it has been possible to dissect although it has been dry for over 100 years. The mouth-parts and other appendages have been mounted on a microscope slide and descriptions and figures of these and of the parts of the shell of the same specimen, taking each variety in turn, form the basis of this paper.

The dried and shrivelled animal parts of some of the barnacles were restored with 1% solution of trisodium phosphate but usually it was found to be sufficient merely to introduce a dilute solution of potassium hydroxide into the shell of the barnacles and leave it for twenty-four hours. The animal parts were then washed out of the shell with distilled water and transferred to lactic acid in which they were dissected. Bubbles of carbon dioxide formed by the interaction of the lactic acid with carbonates helped to inflate the shrivelled parts and could then easily be removed by placing the specimen on a glass slide, covering it with a small piece of thin polythene and stroking this from above with a blunt needle under a stereoscopic microscope. The mouth-parts and various appendages as they were dissected away were mounted in order on a glass slide in polyvinyl lactophenol with lignin pink. Studies of the internal structure of the shell were made from as similar a specimen as possible to the lectotype, the method used being essentially that described by Read (Read, 1960), though sheets of " wet or dry " carborundum paper were used for the grinding and ordinary metal polish for the polishing.

## ***Balanus amphitrite amphitrite*** Darwin

*Balanus amphitrite* Darwin, 1854, p. 240.
*Balanus amphitrite* var. *communis* Darwin, 1854, p. 240, pl. 5, figs. 2*e*, *h*, *l*.
Not *Balanus communis* (Pulteney), 1799, p. 25.
*Balanus amphitrite* var. *denticulata* Broch, 1917, p. 133, text-fig. 14.

*Lectotype.* (Plate 1, *a–g*, Pl. 2, *a–k*.) A complete specimen chosen from about forty others on a piece of bamboo on which the name *Balanus amphitrite* is clearly written in Darwin's writing. Registered No. B.M. 40.9.15.17. Locality Natal, Dr. Krauss. The shell has been left on the bamboo and re-registered—Reg. No. B.M. 1961.12.6.1c, but the opercular valves have been mounted separately (B.M. 1961.12.6.1a). The animal parts have been dissected and mounted on a microscopic slide (B.M. 1961.12.6.1b).

*Paralectotypes*

(1) The remaining barnacles on the bamboo, excluding those which are small and pink in colour which are *B. venustus*, B.M. 1961.12.6.1f (see below)

(2) Similar specimens on a second shorter piece of bamboo which is probably but not certainly part of the same material, B.M. 1961.12.6.3c.

(3) Shells 28 and 29, without opercular valves, listed as " var. *communis* ; ship from West Indies ". B.M. 1961.12.6.6c–7c.

(4) Shells 1, 2, 6 and 7. Listed as " var. *communis* ; ship's bottoms ". All without opercular valves. Locality unknown. B.M. 1961.12.6.8e–11e.

(5) Opercular Valves 4, listed as " var. *communis* (Natal) ". One scutum and one tergum. These are very similar to those of the lectotype and are probably from the same material. B.M. 1961.12.6.12e.

(6) Opercular valves listed as " var. *communis* " ; No. 6, B.M. 1961.12.6.13e. One scutum from Faro ; No. 7, B.M. 1961.12.6.14e. One scutum and one tergum

from "Philippine Arch". No. 11, B.M. 1961.12.6.15e, one scutum and one tergum from Smyrna; No. 15, specimen now missing, from Sydney; No. 2, B.M. 1961.12.6.16e, three scuta and three terga from an unknown locality; No. 3, B.M. 1961.12.6.17e, one scutum and one tergum listed as "pale sub. var." from an unknown locality.

(7) A row of six terga on a slab separate from those in the cabinet labelled *B. amphitrite* of which the first, No. 6, has "var. *communis*" written under it in what may be Darwin's writing. There is no locality for these specimens. B.M. 1961.12.6.18e.

(8) Slab 17.1.7, one complete shell without valves or animal parts and six separated varieties. Labelled by Darwin "*Balanus amphitrite*". B.M. 1961.12.6.22e.

(9) Slab 17.1.10, two large specimens on oyster shells and one or two smaller ones labelled *Balanus amphitrite* by Darwin. B.M. 1961.12.6.23e.

NOTE. Shells now in positions 31 and 34 must have been substituted for the original specimens here as they are both *niveus* and not "*communis*" as they should be, according to Darwin's list.

Pilsbry (1916, p. 55) notes that it was Darwin's habit to give the name *communis* to the typical form of any species that had a number of varieties. The modern procedure however, is to give the type variety or sub-species the same name as the species and in this case what Darwin calls *Balanus amphitrite* var. *communis* should be *Balanus amphitrite* var. *amphitrite*, or if the form is treated as a sub-species as I propose to do, simply *Balanus amphitrite amphitrite*. The name *communis* is in any case inadmissible as it is preoccupied by *Lepas communis* Pulteney which is a synonym of a different species of *Balanus—B. perforatus*.

Darwin did not select a holotype, so that it falls to me to select a lectotype to serve its purpose. It would have been satisfactory to have selected one of the specimens that had been listed by Darwin as "var. *communis*", however, none of these is complete, either the opercular valves are missing or valves are all that remain. None of these specimens have any of the animal parts and very few of them are from known localities. Darwin, p. 246, writes that he has seen specimens of the typical form "var. *communis* from Natal associated with var. *venustus*". The specimens on the bamboo are from Natal, most of them are of the "communis" form while others are of the *venustus* form. There is a large number of complete specimens and Darwin has written *Balanus amphitrite* on the bamboo itself. I, therefore, select one of the *communis*-like specimens on the bamboo to be the lectotype of *Balanus amphitrite* Darwin and, therefore, of *Balanus amphitrite amphitrite*. This is the specimen photographed (Pl. 1, *a–b*). The opercular valves have now been separated and cleaned and the animal parts dissected and the labrum, mandibles, maxillae and both of each of the six pairs of cirri have been mounted in order on a slide and photographs of a selection are given on Pl. 2. A second specimen from the other piece of bamboo was also dissected for comparison and study but has not been figured—I could find no essential differences. The figure of the section of the shell-wall (Pl. 1, *h*) is from a separate, incomplete specimen taken from the first piece of bamboo (B.M. 1961.12.6.4d).

DESCRIPTION

*Size.* The shell of the lectotype (Pl. 1, *a*, *b*) has a greatest diameter of 12·8 mm. and a height measured along the slope of the larger lateral of 12·2 mm. and along the lateral of the opposite side of 5·5 mm., the barnacle having grown much more on one side than the other. The greatest diameter of another specimen on the main piece of bamboo is 17·7 mm. and a specimen on the second piece has the greatest basal diameter of 22 mm. The largest specimen in the collection is one of those on Slab 10 with a basal diameter of 30·2 mm.

*Colour.* The shells of the specimens on the pieces of bamboo including the lectotype have an off-white ground colour with longitudinal dark slate coloured stripes with a slightly violet tinge, a colour which is very similar to that of Darwin's coloured figure, Pl. 5, 2*e*. The number of stripes and their thickness is variable. Those of the lectotype can be seen in the photographs. Most of the shells on the bamboo have stripes which are considerably broader than the white interspaces. There is often a white stripe of extra breadth in the middle of a compartment or at its edges. The stripes are narrower than the interspaces on shells 1, 2, 6 and 7 and the colour of the stripes of shells 2 and 6 is more violet especially towards the base of the shell. The radii are whitish, often with flecks of colour, see below.

*Shape.* The specimens on the bamboo including the lectotype and also " shell 28 " from the West Indies are all very similar in shape to one another and have the profile to the rostrum convex and that of the carina concave. Shells 1, 6, 7 and 29 are of a low conical form with straight profile to the rostrum and are more like Darwin's figure in shape than is the lectotype.

*Parietes.* Pl. 1, *h*, is a photograph of a polished section of one of the parietes. The pattern of the interlaminate figures can be seen without difficulty but is most easily described with the aid of the diagrammatic representation given in Text-fig. 1. This shows a portion of shell-wall sectioned parallel to the base and polished to show the pattern of the interlaminate figures. The pores are large and evenly spaced. The septa (s) between them extend inwards as vertical ribs (r) which may themselves have flutings (f). The portions (d) of the outer lamina which come opposite the pores are dark purplish in colour and more translucent than the rest of the shell. Individual pores, however, such as that marked (p) often situated near the middle of a compartment do not have this dark portion of the outer lamina opposite them. Such a pore may be recognized from the outside by the presence of an exceptionally broad white stripe (w) such as mentioned above under the description of the colour. Running down the sagittal plane of the septum is a nuance, or difference in structure, which is more opaquely white than the rest of the shell substance and in section shows as a white line (a) running down the middle of each septum from the internal rib almost to the outer lamina where it becomes broken up into irregular patches. In the inner lamina, tree-like patterns (b) are produced by off-shoots of opaque white nuances from this line. Each of the internal ribs of the shell-wall contains a part of this tree-like pattern and it can be seen that the fluting of the ribs corresponds with the white branches of the " top of the tree ". The radii are broad and whitish in colour but in the lectotype and some other specimens they are freckled with specks of colour similar to that of the stripes of the shell. These flecks of

colour are in the septa themselves and not in the material which fills the interspaces. They are slightly below the outer surface. The septa have denticuli on their lower sides which are sometimes conspicuous when the sutural edge of the radius is examined but are often blunt, few in number and difficult to see.

The radii of the lectotype and the others on the bamboo and those of the two

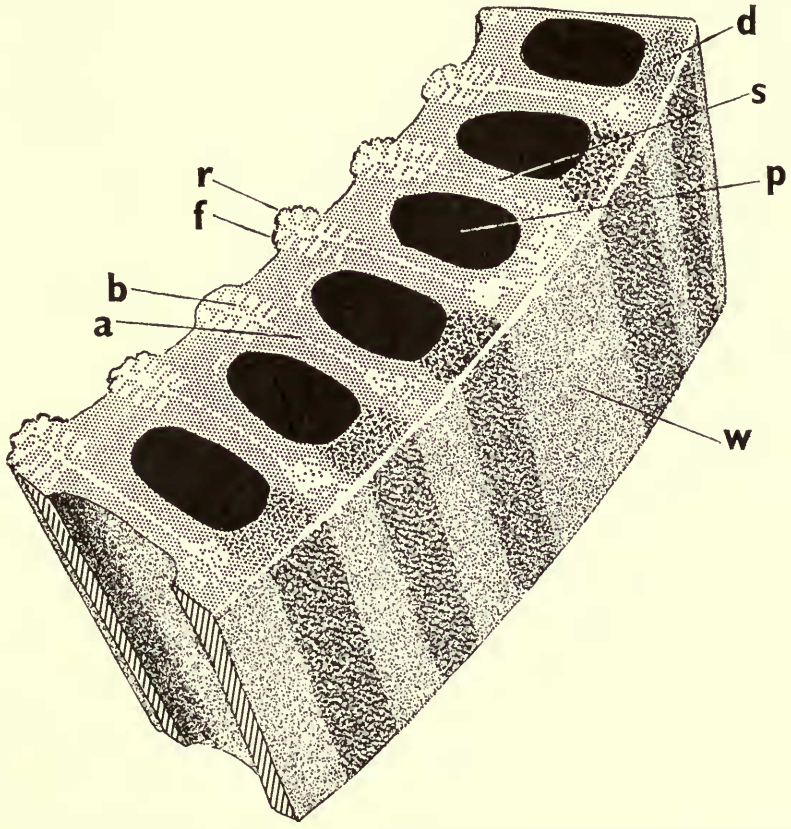


FIG. 1. Piece of parietal wall of *Balanus amphitrite* s. str. sectioned parallel to the basis and polished showing the patterns visible when lit by glancing illumination. Diagrammatic.

(*a*) white line running down septum ; (*b*) " tree-like " pattern ; (*d*) section of coloured shell stripe ; (*f*) fluting to internal rib ; (*p*) pore ; (*r*) rib ; (*s*) septum ; (*w*) extra-wide white stripe. For further explanation see text.

specimens on Slab 10 have summits more or less parallel to the base while the radii of specimens 1, 2, 6, 7, 28 and 29 have more oblique summits.

*The scutum* of the lectotype is shown in Pl. 1, *c–d*. The outer surface is rather smooth with the growth lines visible but not very prominent. The articular ridge is prominent and about half the length of the tergal margin. The adductor ridge is straight and parallel to the occludent margin. The pit for the lateral depressor muscle is very shallow. The internal surface is roughened especially in the apical

half of the valve. The other scuta identified by Darwin as belonging to " var. *communis* " and listed above are all rather similar although some of them have more prominent growth ridges. The scuta and terga of most specimens, including the lectotype are white on the inside.

*The tergum* of the lectotype (Pl. 1, *e, f*) agrees very closely with Darwin's description of that of " the commonest purple-stripe forms " which is detailed and rather long and need not be repeated here (Darwin, 1854, p. 244). Most of the specimens labelled " var. *communis* " by Darwin have a similar short, broad spur and only one or two of them have a narrow spur like that of his figure 2(1).

*The labrum* of the lectotype (Pl. 2, *a*) has twelve or thirteen teeth on each side which continue down into the notch where they gradually become smaller and disappear.

*The mandible and maxilla* are shown in (Pl. 2, *j, k*) and call for no special comment, the maxilla has eight to nine smaller spines between the two pairs of large spines.

*The cirri* shown in (Pl. 2, *b–g*) agree very well with the description given for his var. *denticulata* by Broch (1927, p. 135) including the curved spines on the inner and outer faces of the basal segments of the 3rd cirrus. These are shown in an enlarged photograph in Pl. 2, *h*.

I have placed the var. *denticulata* Broch in the synonymy of *amphitrite* s. str. as such essentials as the teeth on the maxilla and the structure of the 3rd cirrus strongly support this. The shape of the shell described by Broch (1927) is like that of Darwin's figure (Darwin, 1854, pl. 5, 2, *e*) and like some of the paralectotypes especially shells 1, 2 and 7, these all having concave profiles to the rostral plate. The shape of the shells of the lectotype and paralectotypes on the bamboo is rather different as the rostral plates of these have convex profiles. It is possible that this is a growth response to the curved shape of the bamboo.

### ***Balanus pallidus pallidus*** Darwin

*Balanus amphitrite* var. *pallidus* Darwin, 1854, p. 240, pl. 5, figs. 2*c–k*.
*Balanus amphitrite* var. *candidus* Darwin in M.S.

*Lectotype*. (Pl. 3, *a–d*) a selected specimen from Slab 17.1.25, B.M. 1961.12.6.36c, this has been dissected and the valves, B.M. 1961.12.6.36a, and the animal parts, B.M. 1961.12.6.36b, are now on slides. Locality unknown.

*Paralectotypes*

(1) Slab 17.1.25. Several other barnacles remaining on the slab after the lectotype was removed. B.M. 1961.12.6.43c, e, most of them are complete with opercular valves and animal parts. One of them, B.M. 1926.12.6.43d, has been ground to give a section of parietal wall. Locality unknown.

(2) Shell 3. A shell complete with opercular valves but no animal parts. This is the specimen of Darwin's figure (Darwin, 1854, pl. 5, 2*d*), B.M. 1961.12.6.37c. Locality unknown.

(3) Shell 4. A very similar, slightly shorter shell with no valves or animal parts. Locality unknown. B.M. 1961.12.6.38c.

(4) Shell 5. A group of three small shells complete with opercular valves and probably with animal parts. Darwin's manuscript list reads, " on wood W. Indies Brit. Mus.". The specimens are no longer on wood. Two intact specimens B.M. 1961.12.6.39c, one shell with valves B.M. 1961.12.6.39c, animal parts of same B.M. 1961.12.6.39b.

(5) Shell 11. This is a large specimen with a conical shell complete with opercular valves supported on cotton wool but no animal parts. The shell has been deformed presumably by the toxic effect of the copper sheathing of the hull to which it was attached in the way described by Stubbings (1959). This is listed by Darwin as " var. *candidus* from West Coast of Africa ". B.M. 1961.12.6.41c.

(6) Shell 13. A well formed conical shell without valves or animal parts on a portion of a much larger shell of *Balanus tintinnabulum* listed by Darwin as " var. *candidus* on *B. tintinnabulum* on ship's bottom ". B.M. 1961.12.6.42c.

(7) Slab 17.1.26. Two shells attached to one another, one empty and one with opercular valves and probably animal parts. Two scuta and two terga are also mounted on this slab and there are positions where other shells and valves have been attached but are now lost.

(8) Slab 17.1.27. B.M. 1961.12.6.45e. With one complete shell, three pieces of separate parietes, four scuta, five terga and three positions now empty, the pieces having been lost.

(9) Slab 17.1.34. B.M. 1961.12.6.46e. A group of about 10 specimens on the walls of a *Balanus tintinnabulum*, four of these specimens are complete. Mounted on the slab alongside are three scuta and two terga and there is a space for another piece which is now missing. One has provided a section of parietal wall. B.M. 1961.12.6.46d. (Pl. 3, *m*.)

(10) Slab 17.1.37. B.M. 1961.12.6.47e. This contains a piece of wood which no longer has any barnacles on it. Five other specimens which were once attached to the slab are now also missing. There remains one very obliquely grown specimen which is complete, three scuta, one tergum and two minute specimens on a bivalve shell.

(11) Opercular Valves 1. Two scuta and four terga listed by Darwin as " var. *pallidus* ". B.M. 1961.12.6.48e.

The name *pallidus* occurs only once in Darwin's handwriting. This is the entry for this variety in his list of " opercular valves ". In every other case in his list of shells Darwin uses the name *candidus*, that is for shells no. 3, 4, 11, 13. The slabs listed above are also all named " var. *candidus* " in Darwin's handwriting on the back of the slab, written either in pencil or in ink. The name *candidus* is clearly the manuscript synonym of *pallidus*. The specimens agree with Darwin's diagnosis of the variety and one of them, as noted above, is his figured specimen.

*Description.* The height of the lectotype is 13·8 mm. and its greatest diameter is 8·2 mm. The largest specimens are two on Slab 17.1.25, one with a height of 13·8 mm. and diameter of 13·8 mm. at the base and 12·8 mm. at the top and the

other with a height of 13·2 mm., and greatest diameters at the base and top respectively of 13·4 and 11·7 mm. This and nearly all the specimens are of the cylindrical form. Apart from very young specimens the only ones with conical shells are Shell 9 (the distorted specimen), Shell 13, and one of the ten specimens on Slab 17·1·34. Shell 9 has a basal diameter of 17·6 mm. in one direction and 14·4 mm. at right angles to this, and the diameter at the top is 9 mm. × 7 mm., and the height 10·8 mm.

Shell 13 is a conical specimen with a base of 15·3 × 13·1 mm. and aperture of 8·3 × 4·6 mm. and a height of about 9 mm. The one with a conical shape of the ten specimens on Slab 17.1.34 is very similar to the last but is smaller. All the others on this slab are of the cylindrical type.

The shell is white in colour with sometimes a thin purple line along the edges of the parietes. A photograph of the polished section of parietal wall is given in Pl. 3, *m*. It seems to be characteristic of this species to have, in addition to the normal row of large pores, subsidiary smaller pores outside them. There is the usual white line between the major pores and this branches distally to give subsidiary white lines between the subsidiary pores. Between each major pore and the inner face of the wall there is, in section, a white line parallel to the plane of the wall and about the length of the width of the pore; the "tree-like" pattern is sometimes more distinct than in the specimen photographed but it is often more obscure.

The scuta often have a triangular blue-black area both internally and externally as can be seen in Pl. 3, *g* and *h*.

The radii are usually oblique and have inconspicuous striations parallel to the base, the septa being opaquely white and the material between them hyaline white. The denticuli of the septa on the sutural edge of the radius are very inconspicuous.

The scuta on Pl. 3, figs. *g* and *h* are typical with the articular ridge about half the length of the occludent margin. There is a faint ridge running between the articular ridge and the basal margin which fades out at both ends and reaches neither the articular ridge nor the basal margin.

The pit for the depressor muscle is so shallow as to be almost non-existent. Externally the growth ridges are distinct; the apical part of the scutum is roughened on the inside.

The tergum, Pl. 3, *e*, *f*, has a long and narrow spur about its own width distant from the basi-scutal angle. I do not believe the tergum figured by Darwin (1854, pl. 5, 2*k*) is of this species.

The crests for the lateral depressor muscle are well developed and project beyond the basal margin. In addition to the growth lines the external surface shows some longitudinal striations which correspond with the crests for the lateral depressor muscle on the other side of the valve.

The labrum of the dissected specimen, Pl. 3, *j*, has two teeth on each side.

The maxilla, Pl. 3, *l*, has two upper and two lower spines much longer than the others.

The cirri are shown in Pl. 3, *n*–*q*. The 3rd cirrus has short broad segments and is very hairy, Pl. 4, *r*.

### ***Balanus pallidus stutsburi*** Darwin

*Balanus amphitrite* var. *stutsburi* Darwin, 1854, p. 240.

*Lectotype.* (Plate 4, *a–f*; Pl. 5, *a*, *c*, *e–k*), the only complete specimen remaining of those studied by Darwin, one of four specimens on Slab 17.1.12. On the back of the slab in Darwin's writing is "*Balanus amp.*". All four specimens are very similar to Shell 8 which is listed by him as "var. *stutsburi*". The lectotype had written on the shell in ink the old register number 41.1.3.34, which has made it possible to trace the locality from which it came, which Darwin may not have known. It was among material from the West Indies presented by J. E. Gray.

*Paralectotypes*

(1) Slab 17.1.12. The three specimens remaining on this slab after selection of the lectotype. One of these, B.M. 1961.12.6.53, has opercular valves but no animal parts, the other two are empty shells. Other details as above.

(2) Shell 18. This is Darwin's figured specimen (Darwin, 1854, Pl. 5, 2*d*), from a ship from West Africa. Stubbings (1959) describes the distorted condition of the specimen and gives good reason for believing the distortion to be due to the toxic effect of the copper sheathing of the hull to which it was attached. B.M. 1961.12.6.49c.

(3) Shell No. 8. A well-formed empty shell very similar in appearance to those on Slab 17.1.12, "ship from west coast of Africa". B.M. 1961.12.6.50c.

(4) Shells 9, 10, 14, 16 are all empty shells distorted in their growth and very similar to Shell 18. All from a ship or ships from West Africa. Shell 9, B.M. 1961.12.6.55c, had a second broken specimen attached which has been sectioned B.M. 1961.12.6.55d. Shell 10, B.M. 1961.12.6.55e, is a small specimen attached to a piece of mollusc shell with another white barnacle shell alongside it. Shell 14, B.M. 1961.12.6.34e carries three specimens of *B. venustus* as noted in Darwin's M.S. Shell 16 is registered B.M. 1961.12.6.54c.

(5) Shell 12, B.M. 1961.12.6.57c, a whitish empty shell from West Africa.

(6) Slab 17.1.28, B.M. 1961.12.6.58c. Three or four of the specimens half buried under specimens of another species, *B. tintinnabulum*. On the back of the slab in Darwin's writing is "*B. tint.* with *B. amphitrite* var. *stutsburi*", and also written in the same hand at another time "*B. subcostatus* Leach, W. Indies, Rev. L. Guilding". *B. subcostatus* appears to be a manuscript name.

(7) Microscope Slide No. 23 of the University Museum of Zoology, Cambridge. Listed in Darwin's writing as "*amphitrite stutsbury* single specimen" and containing mouth-parts, labrum and cirrus. The mounting medium on the slide was badly shrunk and dark brown in colour, but it has been possible to remount the specimen in polyvinyl lactophenol and the principal parts have been photographed (Pl. 5, *b*, *d*).

(8) Opercular Valves 9. B.M. 1961.12.6.59e, two scuta and four terga.

(9) Opercular Valves 10. B.M. 1961.12.6.60e, one scutum and one tergum.

[Shell No. 17 is listed as "var. *stutsburi* West Africa". This was a complete specimen but with the shell very mucl distorted by crowding and from the shell

alone difficult to determine. Examination of the opercular valves, labrum and 3rd cirrus leave no doubt that it is not *stutsburi* but a specimen of *Balanus amphitrite* s. str.]

The lectotype is a very fine and typical specimen, one of the few in the type collection with the shell undistorted in its growth and the only one complete with animal parts as well as valves and shell, but I have hesitated before selecting it as it comes from the West Indies, and Darwin wrote (Darwin, 1854, 246), " all the specimens which I have seen have come on shells or on ships' bottoms, from West Africa ". Now Darwin must have seen not only the lectotype but also the specimens on Slab 17.1.28 which are also from the West Indies, for the slabs have his writing on the back. He may not have known that the lectotype and others on Slab 17.1.12 came from the West Indies; but Slab 17.1.28 has " West Indies " and also " var. *stutsburi* " in his own writing. I am indebted to my colleague Miss B. M. Skramovsky for confirming that the writing is Darwin's. It is therefore my duty under Recommendation 72E of the International Code of Zoological Nomenclature (Stoll *et al.*, 1961) to correct the type-locality, erroneously restricted to West Africa, to include the West Indies. Having done so I am free to select the lectotype designated above.

## Description

*Size.* The greatest diameter of the base of the lectotype is 17·3 mm. and its height is 9·5 mm. Specimen B of this group measures 18·5 mm. and 11·1 mm. respectively and a third specimen 18·6 mm. and 12·6 mm. The specimen of Darwin's figure *2d* is smaller—11·3 mm. in diameter and 8·1 mm. high.

*Colour.* The upper part of the shell is usually white and the lower part coloured by pinkish purple stripes which coalesce.

The radii are conspicuously white and have oblique summits.

*Shape.* The undistorted specimens are conical with a straight rostrum and straight or concave carina, the carina being distinctly higher than the rostrum.

*The parietes.* The photographs (Pl. 4, *g*, *h*) show sections of parietes which seem to be typical of this subspecies and very similar to sections of *pallidus*. In addition to the normal row of large pores there are subsidiary small pores outside them more or less opposite the septa. Immediately around the pores the shell substance is white and outside both the large and small pores there is in those parts of the shell where the coloured stripes coalesce a crescent of purple colour. Between each pore and the inner face of the parietes there is in section a white line parallel to the plane of the wall and about the length of the width of the pore. The " tree-like " pattern is rather obscure in the specimen photographed but the elements are there and in other specimens examined they are more like those specimens of *B. amphitrite* s. str.

The radii have inconspicuous denticles to the lower edge of the septa on the sutural margin. The shell material filling the interspaces is more hyaline than the opaquely white septa.

The scutum of the lectotype (Pl. 4, *c*, *d*) and the others from Slab 17.1.12 have externally a dark blue-black triangular area bounded by white borders on the scutal

and occludent margins. The growth lines are moderately developed, the roughness of the inner surface of the apical part of the valve between the articular ridge and the occludent margin is in the form of rough longitudinal ridges. The base of the articular ridge continues towards the base of the valve as a low rounded ridge passing very near to the shallow impression of the lateral depressor muscle and between this and the adductor ridge is another faint ridge.

The tergum usually has a long and narrow spur at about its own width distant from the basi-scutal angle (Pl. 4, *e*, *f*). The crests for the lateral depressor muscle are well developed and project beyond the basal margin. In addition to the growth lines the external surface shows some longitudinal striations which correspond with the crests for the lateral depressor muscles on the other side of the valve.

The labrum of specimen A (Pl. 5, *a*) has only one tooth on each side. That of Darwin's dissection now in the University Museum of Zoology, Cambridge (Pl. 8, *b*) has three and I believe this to be the more normal condition.

The mandible is shown in Pl. 5, *e*, but I can see nothing remarkable about it.

The maxilla of specimen A (Pl. 5, *c*) has weakly developed spines, the two pairs of strong spines being hardly larger than the others. That of the University Museum of Zoology, Cambridge specimens (Pl. 5, *d*) also has rather weaker spines but I have seen maxilla of this subspecies with normally developed spines.

The cirri are shown in Pl. 5, *f*, *g*, *h*, *i*, the 3rd cirrus has very short, broad segments and is very hairy (Pl. 5, *h*, *k*).

Apart from the colour difference I have been unable to find a satisfactory way of distinguishing *stutsburi* from *pallidus*. The following features are characteristic of both and usually separate them from the other forms: the very long spur to the tergum, the presence of supplementary pores in the parietes and the triangular dark patch on the scutum. In order to draw attention to the similarity I am, in this paper, treating them as belonging to the same species. Unfortunately, the rules do not permit the name of this species to be *stutsburi* with *pallidus* as its pale subspecies, for the name *pallidus* has line priority over *stutsburi* in Darwin's monograph. The name of the species must therefore be *Balanus pallidus* and *stutsburi* is a coloured subspecies.

### ***Balanus venustus venustus*** Darwin

*Balanus amphitrite* var. *venustus* Darwin, 1854, p. 250, pl. 5, fig. 2*a*.

*Lectotype*. Pl. 6, *a–g*, *j–p*. A complete specimen, Reg. No. B.M. 1961.12.2.24c, selected from the same piece of bamboo as the lectotype of *Balanus amphitrite* s. str. The shell was growing on a specimen of the latter sub-species and remains there but the opercular valves have been removed and mounted on a slide (Reg. No. B.M. 1961.12.6.24a) and the animal parts have been dissected and mounted in polyvinyl lactophenol on a second slide, Reg. No. B.M. 1961.12.6.24b. Locality: Natal, Dr. Krauss.

*Paralectotypes*

(1) About fifteen other small pink barnacles on the main piece of bamboo. The shell of one of these B.M. 1961.12.6.25d, is sectioned and shown in Pl. 3, *d* (there are no specimens of this subspecies on the second, shorter piece of bamboo).

(2) Specimens on Slab 17.1.21 (Reg. B.M. 40.9.30.64–65) : B.M. 1961.12.6.26e, a group of four, two of them complete with opercular valves and one perhaps still with animal parts ; a particularly well grown separate specimen without valves; three separate scuta ; four terga and three parietes one of which, B.M. 1961.12.6.26d, had been sectioned. Locality : Good Hope, Dr. Krauss.

(3) Shell 15. A large specimen from Ceylon without valves, B.M. 1961.12.6.27c.

(4) Shell 19. A specimen, B.M. 1961.12.6.28c, listed as " var. *venustus* (with var. *communis*) Natal ", there is no sign of the var. *communis* now. No valves.

(5) Shell 20. B.M. 1961.12.6.29c. Listed as " do. on an *Ostrea* ". (" do." being the abbreviation for " ditto " for " var. *venustus* "), but there is no sign of the oyster. No valves. Natal.

(6) Shell 30. B.M. 1961.12.6.30c. This is the specimen of the " var. *venustus* " figured in Darwin's monograph (Pl. 6, 2*a*), although according to the list it is " var. *communis* ", clearly the correspondence between the present arrangement of the specimens and the list is imperfect.

(7) Opercular valves 5. A scutum and a tergum. B.M. 1961.12.6.31e.

(8) Opercular valves 13. A scutum, Natal. B.M. 1961.12.6.32e.

(9) Slab 17.1.30. Reg. No. B.M. 1961.12.6.33e. Several specimens mostly empty on two conical mollusc shells. Locality : Algoa Bay, Dr. Stanger. One sectioned, B.M. 1961.12.6.33d.

(10) Shells 14. Two empty shells, B.M. 1961.12.6.34c, on a specimen of *Balanus amphitrite stutsburi*. Ship's bottom from West Africa.

(11) Shell 17. Two small complete specimens B.M. 1961.12.6.35c on a specimen which is listed as *B. amphitrite stutsburi* from West Africa ; but is in fact *B. amphitrite* s. str.

I have selected the lectotype from the material on the bamboo as there are more specimens here than in any other group to choose from. The specimens were undoubtedly seen by Darwin and although he has left no definite indication of naming them var. *venustus* he must have recognized them and considered them when writing his monograph, and they will be the specimens of this variety from Natal associated with var. *communis* which he refers to on p. 246.

DESCRIPTION

*Size.* The greatest diameter of the base of the lectotype is 8·9 mm. None of the other specimens on the bamboo is as large as this. By far the largest specimen is Shell No. 15 from Ceylon with the basal diameter of 14·8 mm. The next in size is one on Slab 21 from West Africa which measures 10·9 mm. Nearly all the other specimens in the collection are smaller than the lectotype.

*Colour.* The ground colour is white or slightly pinkish and the walls are ornamented with about forty evenly spaced stripes. The stripes of the lectotype are purplish pink. Shell No. 30 (the specimen of Darwin's fig. 2*a*) is of a paler pink and

considerably paler than it is represented in the coloured figure of the monograph. Some of the paratypes on the bamboo however have stripes of as dark a red as this figure shows.

The radii of the lectotype are of the same colour near the parietes as the stripes, becoming gradually paler towards the edges. Most of the radii are coloured in this way but sometimes the pinkish colour near the parietes is broken up into one or two stripes. In contrast to the position in *B. amphitrite* s. str. any colour in a radius of *venustus* is in the material filling the interspaces between the septa which are themselves white in colour.

*Shape.* The profile of the rostrum is nearly always convex and that of the carina is usually concave. The summits of the radii may be parallel to the base but often they are oblique leaving the upper parts of the alae exposed.

*Parietes.* An immediate difference between *Balanus venustus* and *Balanus amphitrite* becomes apparent if a section of a parietal wall is examined (Pl. 6, *h*) ; the coloured stripes come opposite the septa between the pores instead of opposite the pores themselves. Otherwise the pattern visible on the polished surface of a section is very similar in the two species. There are the same tree-like outgrowths running into the ribs from the white line running down the middle of the septum. The other, outer, end of this line often runs into the pink patch which is the section of the stripe, bifurcating it on its inner side. On the sutural edges of the radii the septa have conspicuous denticuli projecting from their lower sides. Unless care is taken with the illumination when examining the edge of the radius, the shadows cast between the denticuli make it difficult to see that the spaces between the septa are filled up solidly ; and the fact that the filling material is often more darkly coloured than the septa adds to this difficulty.

*The scutum* of the lectotype is shown in Pl. 6, *d*, *e*. It is very similar to that of *Balanus amphitrite* but has a distinct tinge of purple colour in its substance. This colour in some of the paralectotypes is pink rather than purplish. The articular ridge is more than half the length of the outer margin and continues towards the base as a low ridge well clear of the pit for the lateral depressor muscle.

*The tergum* differs in colour from that of *Balanus amphitrite* s. str. in the same way as the scutum. The spur is much closer to the scutal margin and the carinal half of the valve is less developed than the scutal half so that the carinal edge is very much shorter than the scutal edge, or in Darwin's words, " The carinal half of the basal margin is much hollowed out ". The crests for the depressor muscles are well developed and project beyond the margin, they have been damaged in the lectotype (Pl. 6, *f*, *g*).

*The labrum* of the lectotype (Pl. 6, *c*) has three large teeth on each side and the notch is smooth.

*The mandible and maxilla* (Pl. 6, *n*, *o*) have no special features distinguishing them from those of *Balanus amphitrite* s. str., except that the maxilla has only five small spines between the two pairs of large spines.

Four of the six pairs of cirri are shown in Pl. 6, *j–m*, but the only difference I could find between these and those of *B. amphitrite* was in the 3rd cirrus (Pl. 6, *p*) which appears to lack the curved spines on the inner and outer faces.

## *Balanus venustus niveus* Darwin

*Balanus amphitrite* var. *niveus* Darwin, 1854, p. 240, pl. 5, fig. 2*f*.

*Lectotype.* (Pl. 7, *a*, *b*, *d–h*, *l–r*.) One of the specimens on Slab 17.1.29. Reg. No. B.M. 40.4.5.59, now registered B.M. 1961.12.6.61c. The animal parts were still inside this shell and have now been dissected and mounted on a slide, Reg. No. B.M. 1961.12.6.61b. The valves had, however, been removed but are presumably those mounted separately on the same slab. These are now on a separate slide, Reg. No. B.M. 1961.12.6.61a. Locality : Madagascar.

*Paralectotypes*

(1) A group of five B.M. 1961.12.6.62e fully grown and two very much smaller specimens on the same slab (17.1.29). Two of these have no opercular valves and none has animal parts. The parietes of one of this group have been sectioned. B.M. 1961.12.6.62d.

(2) " Shell " 32. An empty shell which is the specimen on pl. 5, fig. 2*f* in Darwin's Monograph ; from the West Indies. B.M. 1961.12.6.63c.

(3) Shell 33. Part of a large specimen consisting of the rostrum, the right lateral and some of the basis, from Madagascar. B.M. 1961.12.6.64c.

(4) Shell 36. A whitish shell without opercular valves, from Madagascar. B.M. 1961.12.6.65c.

(5) Shell 35, an empty shell listed as " var. *niveus*, coast of Portugal ". B.M. 1961.12.6.68c.

*Other material*

(1) Shell 31, an empty shell very similar to Shell 32 and certainly a *niveus* but not strictly a paralectotype as position 31 is listed as " var. *communis* ". This shell has provided the sections shown in Pl. 7, *j*, *k*. B.M. 1961.12.6.66d.

(2) Shell 34, a very similar empty shell to Shell 31 and also listed as *communis*. B.M. 1961.12.6.74a.

(3) Opercular valves 12, a scutum and a tergum. B.M. 1961.12.6.67e. According to the list these are " var. *niveus* (West Indies) ", but they do not seem to be typical.

The only specimen with animal parts has been chosen as the lectotype and the opercular valves which were mounted beside them are assumed to have come from this specimen.

### Description

*Size.* The greatest diameter of the lectotype is 8·4 mm. The length of the left lateral 8·2 mm. and the right lateral 4·3 mm. The basis of the largest paratype measures 11 mm. but the two parietes left of Shell 35 must have belonged to a larger specimen than this.

*Colour.* All the specimens are white with numerous narrow colourless hyaline stripes. The opercular valves of the lectotype are white with traces of deep purple

coloured epidermis on the inside. The opercular valves No. 12 mounted by Darwin have a slightly bluish tinge and the traces of epidermis are a dark blue-grey.

*Shape.* Very similar to that described above for *B. amphitrite* s. str. and for *B. venustus venustus* but the summits of the radii of all the specimens are oblique.

*Parietes.* A polished section of a piece of parietes (Pl. 7, *j*, *k*) shows a pattern basically as that of *B. amphitrite* s. str., but there is no colour and the narrow hyaline stripes of the shell correspond to the septa between the pores.

The sutural edges of the radii of " Shell 33 " have distinct denticuli on the lower sides of the septa. The septa are of a more opaque-white than the shell substance filling the interspaces.

*The scutum.* (Pl. 7, *f*, *g*.) The angle between the tergal and basal margins is rather sharp in the right scutum of the lectotype and less so in the left. The articular ridge is more than half the length of the tergal margins and the slight ridge running from it curves asymptotically to the basal margin away from the pit for the lateral depressor muscle. The scutum of Opercular Valves 12 has a very short articular ridge considerably less than half the length of the total margin and the ridge running from it between the basal margin is very faint and there is no pit for the lateral depressor muscle.

*The tergum* (Pl. 7, *d*, *e*), which is presumably from the lectotype has been damaged. It is very like that of *B. amphitrite venustus* with the spur close to the scutal margin and the carinal half of the basal margin much hollowed out. The crests for the depressor muscles project well beyond the basal margin. The tergum of Opercular Valves 12 has a long and narrow spur and the crests for the depressor muscles are hardly developed.

*The labrum and mandible* (Pl. 7, *l*, *h*) are very similar to those of *B. amphitrite venustus*. The labrum of the lectotype has three teeth on each side. The maxilla of the lectotype (Pl. 7, *m*) has the lower part of the inner edge slightly protuberant and bears the lower two large spines. The angle below this is square. There are five smaller spines between the two large pairs of spines.

*The cirri* of the lectotype (Pl. 7, *n–r*) call for no special comment.

*The rami* of the 3rd cirrus bear curved hooks (Pl. 7, *r*) rather like those of *Balanus amphitrite*.

### ***Balanus venustus modestus*** Darwin

*Balanus amphitrite* var. *modestus* Darwin, 1854, p. 240.

*Lectotype.* (Pl. 8, *a*, *b*, *d–p*.) A specimen selected from a group of barnacles on the shell of a fasciolariid gastropod mounted on Slab 17.1.19. The barnacle is complete with opercular valves and animal parts. The shell Reg. No. B.M. 1961.12.6.69e remains on the mollusc shell but the valves are now separated (Reg. No. B.M. 1961.12.6.69a) and the dissected appendages are on a microscope slide Reg. No. B.M. 1961.12.6.69b.

Locality probably the West Indies area or the American coast from Florida to Texas.

*Paralectotypes*

(1) About 20 other specimens on the same gastropod shell B.M. 1961.12.6.70e. Only three or four of these still have the opercular valves and there are also specimens of *B. amphitrite niveus* amongst them. The parietes of one of these paratypes has been sectioned. B.M. 1961.12.6.71d and B.M. 1961.12.6.72d.

(2) Two empty shells on the upper valve of an oyster shell, B.M. 1961.12.6.73c, the lower half of which is still on the fasciolariid shell referred to above. These two shells are listed by Darwin as " Number 27 var. *modestus* on a univalve ".

(3) Opercular Valve 8. One tergum. B.M. 1961.12.6.84.e

(4) Cambridge microscope slide 158 with mouth parts and cirri dissected and mounted by Darwin now in the Museum of Zoology, Cambridge ; listed by Darwin as " 158. *B. modestus* var. of *B. amph.* ? do. - do.". The " do. - do." refers to " 1, 2, 3, 6 cirri . . . all trophi ".

All this material is from the one source : barnacles growing on the fasciolariid gastropod from a locality unknown to Darwin. My colleague, Mr. S. P. Dance, has however kindly examined the mollusc shell for me and has been able to identify it as *Leucozonia nassa* Gmelin, a species which is common among rocks at low tide from Florida to Texas and the West Indies.

## Description

*Size.* The lectotype cannot be measured accurately as it is too closely surrounded by other specimens. The greatest dimension of the base is about 7·5 mm. The largest specimen reaches 8 mm. in basal diameter.

*Colour.* In Darwin's words, " Upper part of shell white, lower part uniformly bluish-grey ". Most of the specimens including the lectotype show no trace of stripes but a few specimens have the bluish-grey colour confined to narrow vertical stripes. The bluish-grey colour is confined to the parietes, and valves and radii are white. There is a tendency for all the parietes including the carina to have convex profiles so that the shell has the shape of an inflated, truncated cone.

*The radii* are broad with oblique summits. Many of the specimens but not the lectotype have a conspicuous ribbing parallel to the base on the external surface of the radii.

*Parietes.* A polished section of a parietes is very similar to one of *B. amphitrite* s. str. (Pl. 8, *c*). If the example is one without stripes the bluish-grey colour of the shell permeates most of the shell substance. A stripe, if any are present can be seen in section in addition to the bluish-grey background as a crescent of dark purple brick colour embracing the outer half of the section of a pore.

I have not been able to examine the sutural edges of more than one or two radii where the septa were seen to have inconspicuous denticuli in the lower sides. The septa were more opaquely-white than the substance filling the spaces between.

*The scutum* of the lectotype (Pl. 8, *d*, *e*) has an articular ridge distinctly longer than half of the scutal margin and from it a slight ridge runs towards the basal margin between the pit for the lateral depressor muscle and the adductor ridge. The tergal margin makes a distinct though obtuse angle with the basal margin.

The pit for the lateral depressor muscle is small but deep and opens on to the basal margin.

*The tergum* of the lectotype (Pl. 8, *f*, *g*) has a short spur near to the scutal margin. The crests for the depressor muscle extend beyond the scutal margin. The internal surface is roughened.

*The labrum* (Pl. 8, *p*) has three teeth on each side, two of them being close together on the edge of the notch.

*The mandible* (Pl. 8, *k*) has a rather large upturned 3rd tooth.

*The maxilla* (Pl. 8, *j*) has five spines between the two pairs of large spines and the spines of the lower large pair are a little larger than those of the upper large pair.

*Four cirri* of the lectotype are shown in (Pl. 8, *k*, *l*, *m*, *n*) with an enlargement of part of cirrus 3 in Pl. 8, *o*. The spines on the inner and outer faces of this cirrus are similar to those of *B. amphitrite* s. str. but less conspicuous.

### ***Balanus venustus obscurus*** Darwin

*Balanus amphitriate* var. *obscurus* Darwin, 1854, p. 241, pl. 5, fig. 2*g*.

*Lectotype* (Pl. 9, *a–n*, *q*) a specimen on a segment of crustacean limb from Slab 17.1.22, which was complete with opercular valves and animal parts. Locality, Jamaica, Mus. Leach. Reg. Nos. Shell B.M. 1961.12.6.75c, valves B.M. 1961.12.6.75a, animal parts, B.M. 1961.12.6.75*b*.

*Paralectotypes*

(1) Three other specimens on the same slab also complete with valves and possibly animal parts, also one parietal wall and two terga. B.M. 1961.12.6.76e.

(2) Three parietes from the slab kept separately B.M. 1961.12.6.c.

(3) Two further parietes from the same slab which have been sectioned B.M. 1961.12.6.76d and B.M. 1961.12.6.77d.

(4) Shell 23 listed as " var. *obscurus* on patella local. Unknown ". All that remains now is three separate pieces of parietal wall, B.M. 1961.12.6.78a, and one that has been sectioned, B.M. 1961.12.6.78d.

(5) Slab 17.1.3. Eleven specimens on a pebble from an unknown locality " M. Cuming ". B.M. 1961.12.6.79c.

There are some specimens in Darwin's list which are not now available. " Shell 38 var. *obscurus* hab. unknown C.D." is now missing, and none of Opercular Valves 14 remains. Shells 26 are undoubtedly of *Balanus perforatus* and cannot be the original specimen of " var. *obscurus* loc. unknown " that Darwin placed here.

I have chosen the specimen on the segment of crustacean limb for the lectotype as it is one of the complete specimens from a known locality and is a specimen which is easily specified, it also agrees very well with Darwin's description.

*Size.* The base of the largest intact specimen which is the lectotype has a greatest diameter of 6·7 mm. The specimens on a pebble are too crowded to be measured, but at least three of them are 12 mm. across or more.

*The colour* of the lectotype is pale grey with narrow dark grey longitudinal stripes.

There are more stripes near the basis of the shell than near the orifice for two reasons : (i) there is a tendency for the stripes to be split towards the base, and (ii) for additionally thin lines to appear between them. There is sufficient contrast between the ground colour of the stripes for the latter to be quite distinct in the lectotype and other shells on Slab 17.1.22; but the parietes of Shell 23 have very indistinct stripes and the contrast between the background and the stripes is very slight; the central portions of the wall are dark and parts near the margins, particularly near the basis are pale. The background colour of the central portion is much darker than are the stripes of the pale marginal portions.

*The radii* which have summits at about 45° are closely ribbed horizontally and also ribbed to a lesser extent vertically. The small rectangles between the vertical and horizontal ribs are often reddish in colour, the ribs themselves being white.

The shape is very similar to that described above for *venustus* and *niveus* but the orifice is rather small.

*The parietes.* The horizontal section of parietal wall near the base (Pl. 9, *o*, *p*) shows that there are here more stripes than there are pores. There is a stripe opposite each septum and in addition there are usually thinner stripes between these. There are the usual white lines running down the middle of each septum from the coloured patch-like section of a stripe at one end to the tree-like pattern in the internal rib, at the other end. A similar white line runs from each of the subsidiary stripes inwards towards the pore and leads to a smaller tree pattern in a rib not in the inner wall but inside the pore itself. The pores are thus partly divided into two by subsidiary ribs. Sometimes there are two such ribs in a single pore dividing it into three. Each stripe therefore corresponds to a rib and the rib may either be in the normal place on the inner wall of the parietes or it may be inside a pore.

In addition to the pattern so far described there are often crescents of reddish brown similar to those of *modestus* outside the pores or portions of pores. These crescents can be seen in Pl. 9, *p*; the clearest example being opposite the middle portion of the tripartite pore in the centre of the picture. The pattern in *obscurus* is interesting as it combines the pattern of *amphitrite* s. str. with that of *venustus* s. str. Like *venustus* the stripes seen on the outside of the shell correspond with the septa between the pores and like *amphitrite* the pores have pigment outside them, only in *amphitrite* this pigment is seen from the outside as stripes and in *obscurus* it is too deep to show externally.

The sutural edges of the radii of the disarticulated Shell 23 have very conspicuous, and occasionally ramifying denticuli on the lower sides of the septa. The septa are white and the substance filling the interspaces is pale bluish-grey, like the stripes of the shells. The denticuli are very inconspicuous in other specimens.

*The scutum* of the lectotype (Pl. 9, *c*, *d*) has a very long articular ridge more than two-thirds the length of the tergal margin; otherwise it is very similar to that of *venustus* or *niveus*.

*The tergum* of the lectotype (Pl. 9, *e*, *f*) is also very similar to that of *venustus* and *niveus* with the spur very close to the scutal margin and the carinal half of the valve much less developed than the occludent half.

*The labrum* (Pl. 9, *n*) of the lectotype has three teeth on each side of the notch, the two inner teeth being closer together. The labrum again shows no difference between this form and *venustus* and *niveus*.

*The mandible and maxilla* (Pl. 9, *e*, *m*) call for no special comment. There are five spines between the two large pairs of large spines on the maxilla.

*The cirri* as shown in Pl. 9, *g–k* are very similar to those of *niveus*. The details of the 3rd cirrus of *obscurus* are so similar to those of *niveus* that I have had to re-examine the specimens to make sure that the photographs of the 3rd cirrus of *obscurus* (Pl. 9, *q*) and of *niveus* (Pl. 7, *r*) are really of these two forms respectively and not, as could easily be thought, two photographs of the same specimen.

## ***Balanus variegatus*** Darwin

*Balanus amphitrite* var. *variegatus* Darwin, 1854, p. 241.

*Lectotype*

A large specimen on Slab 17.1.31 from Sydney with opercular valves loose in the shell but no animal parts (Pl. 10, *a*). This specimen was first labelled by Darwin " var. *cirratus* " in ink but this has been crossed out in his writing in pencil and " var. *variegatus* " substituted. This specimen had 187–40.9.22.283 in ink written on it but I can find no trace of this in the Museum register.

The specimen has been re-registered : the parietes and base, B.M. 1961.12.6.80e ; the valves, B.M. 1961.12.6.80a, and the sectioned wall which is from the same specimen, B.M. 1961.12.6.80d.

*Paralectotype*

(1) Material on microscope slide No. 151 of the Zoology Museum, Cambridge. This is in rather poor condition but with the mouth-parts and a few cirri clearly visible (Pl. 10, *g–k*). This is listed by Darwin as " 151 *B. variegatus* do.–do.". The " do.–do." being an abbreviation for " 1, 2, 3, 6 cirri . . . all trophi ".

(2) Opercular Valves No. 16. A broken scutum and a tergum from New Zealand. B.M. 1961.12.6.81e.

*Other material*

1. Slab 17.1.33. B.M. 1961.12.6.87e. Labelled by Darwin " *B. amphitrite* var. between *obscurus* and *variegatus* ". Four shells complete with opercular valves and probably animal parts, one of these has now been dissected, four empty shells, one of which I have sectioned, two parietal walls, four scuta and one tergum.

(2) Shell 24. B.M. 1961.12.6.88c listed as " do. passing into var. *variegatus*. Ship's bottom taken in E. Australia ", the "do." being " ditto " for " var. *obscurus* " in the line above. An empty shell very similar to those on Slab 17.1.33. These are all undoubtedly the specimens from H.M.S. " Fly " referred to by Darwin (1854, p. 246).

DESCRIPTION

*Size.* The greatest diameter of the specimen from Sydney is 17 mm. The specimen from which the appendages on the slide in the Cambridge Museum were taken must have been much smaller than this.

*Shape.* The only specimen now available is not typical as Darwin describes the shape as conical and this specimen is rather barrel-shaped. The summits of the radii are oblique.

*Colour.* The ground colour of the shell is cream with a tinge of pink and the numerous stripes are slaty blue at the base, becoming claret red between the basis and freckled with cream transversely in the way shown in the photograph.

*Parietes.* The section of a right lateral near the base is shown in Pl. 10, *f*, the pores are numerous, round and even, and the pattern of the polished shell of the section is much like that of *B. amphitrite* s. str. with the pigment rather broken up as might be expected from the freckled nature of the stripes.

The sutural edges of the radii have short, blunt denticuli on the lower sides of the septa. There are flecks of purple in the material which fills up the interspaces but the septa themselves are white.

*The scutum* (Pl. 10, *b*, *c*) has a short but distinct adductor ridge. The pit for the lateral depressor muscle is deep and well defined but is open towards the basal margin. Externally there are longitudinal striae as well as the transverse growth lines.

*The tergum* (Pl. 10, *d*, *e*) has a moderately short spur which tapers slightly and is well away from the basiscutal angle. The crests for the depressor muscles are comparatively few in number and rather short.

*The mouth-parts* can be described only from the Cambridge specimen.

*The labrum* (Pl. 10, *g*) has three teeth on each side of the notch.

*The maxilla* (Pl. 10, *i*) has the lower part which bears the lower of the two pairs of large spines forming a distinct projection of the inner edge. The first and second cirri and parts of other cirri, which is all there is preserved on the slide, show no special features.

I have also examined the material from H.M.S. " Fly " referred to above, which Darwin considered to be intermediate between *obscurus* and *variegatus* and which therefore cannot be treated as type material for *variegatus*.

To me these specimens belong to *B. variegatus*, all five of the terga I have examined are very like those of the lectotype of this species. The stripes on the shells are broken up into flecks of colour and one of the maxillae of the dissected specimen has a projecting lower portion of the inner face. Darwin did not give his reasons for placing these specimens near to *obscurus* presumably because of the rather numerous dark grey stripes on a paler grey background. The colour alone is not in my opinion sufficient to indicate affinity with *obscurus* in the absence of other evidence and in the face of the difference in the tergum, and as regards the numerousness of the stripes this is a character shared with *B. variegatus* (see Pl. 10, *a*). Examination of the ground section of the shell of one of these H.M.S. " Fly " specimens also supports my view that these can be identified as *B. variegatus*. The pores are all simple—one to each stripe and not subdivided as they are in *B. venustus*

*obscurus* and the colour of the flecks in the shell substance opposite the pores is reddish purple as it is in *B. variegatus*. *B. venustus obscurus* only has grey here. The mandible is rather different from either and so is the labrum which in the dissected specimen has four teeth on each side.

### ***Balanus variegatus*** var. ***cirratus*** Darwin

*Balanus amphitrite* var. *cirratus* Darwin, 1854, p. 241, pl. 5, fig. 2*b*.

*Lectotype* (Pl. 10, *l*) a large specimen on a gastropod shell on Slab 17.1.35 without opercular valves or animal parts, with Darwin's writing on the back of the slab " *Bal. amphitrite* var. *cirratus*. Mouth of Indus ", B.M. 1961.12.6.82c.

*Paralectotypes*

(1) Slab 17.1.35. Five empty shells without valves on a second gastropod on the same slab as the lectotype. B.M. 1961.12.6.82e.

(2) Slab 17.1.16. About half a dozen empty shells and parts of shells on a similar but larger gastropod shell (Pl. 10, *m*). B.M. 1961.12.6.82e. " *Bal. amphitrite* var. *cirratus*. Mouth of Indus ".

None of the specimens has valves or animal parts and Shell 37 of Darwin's list is now missing.

*Size*. The greatest basal diameter of the largest specimen is 13·5 mm. The colour of most of the shells is buff rather than " very pale purplish brown " described by Darwin, with " indistinct longitudinal brownish stripes transversely flecked with white ". The brown colour in most cases being approximately that of medium oak. The lectotype has, however, a distinctly pink tinge.

*The shape* of the shell is similar to that of *B. venustus* with a convex rostrum and a concave carina, the latter often projecting slightly outwards like the spout of a jug. None of the present specimens have the cup-like bases that Darwin described as being typical of the variety.

*The radii* have oblique summits and are usually horizontally ribbed with slaty-blue lines. I have been unable to see the sutural edges of the radii well enough to be able to describe the septa.

*The parietes*. As Darwin remarks the walls are thin and a section of the parietes shows that the pores are comparatively large. The pattern seen on the polished surface of the section is of the normal type of *B. amphitrite* s. str. with the stripes coming opposite the pores. As seen in Pl. 10, *n*, the pattern between the pores and the outer face is broken up in places by opaque white flecks running inwards from the outer surface. These seem to correspond with the transverse freckles of white on the shells.

All that remains of Darwin's material is quite inadequate for a proper description of *cirratus*. Not only are there no valves or animal parts but none of the specimens now available have the cup-formed shape of the bases. Darwin when discussing his decision to place the various varieties under the one specific name *B. amphitrite* wrote that he had more doubt regarding the *cirratus* than on any other and was

inclined to give it separate specific status; but to me there is very little or no difference between it and *variegatus*.

The peculiar features Darwin stresses are :

1. The peculiar colour. 2. The bases having the cup-formed shape. 3. Beaded growth lines on the scuta. 4. He also notes that the maxillae have the corner extremely prominent.

To take these in turn : 1. The colours of the specimens now extant with Darwin's own written identifications of *cirratus* and *variegatus* overlap. 2. None of the specimens of *cirratus* has the peculiar cup-formed basis, but the specimen of *variegatus* Pl. 10, *a*, has. 3. Beaded growth lines on the scuta might provide a valid difference though Darwin writes that he has seen traces in the common variety. Unfortunately there are no scuta of *cirratus* now available for study. None of the specimens labelled *variegatus* has beaded scuta. 4. The prominent lower corner of the maxilla does not separate *cirratus* from *variegatus* for the latter, like specimens of *niveus*, tends to have a maxilla like this.

No one who has worked on barnacles during the last hundred years can have failed to be impressed by the quality of Darwin's monumental work and it seems anomalous that I should be unable to distinguish his var. *cirratus* from his var. *variegatus* especially as *cirratus* was the variety he was most inclined to separate from all the others and raise to specific rank. The discrepancy can only be accounted for by the absence today of sufficient type material. Of the var. *cirratus* only empty shells remain and as Darwin emphasized repeatedly, sessile cirripedes cannot be identified satisfactorily without an examination of the opercular valves.

## DISCUSSION

In this paper I have divided Darwin's varieties of *Balanus amphitrite* into four separate species. This seems to be the simplest way of expressing my views concerning the affinities between them. First there is *Balanus amphitrite* itself characterized by the presence of numerous teeth on the labrum running down into the notch and by a short stout spur to the tergum not very close to the basi-scutal angle. Secondly, *Balanus pallidus* characterized by a very long spur to the tergum with *B. pallidus stutsburi* as a coloured variety or subspecies. Thirdly, *Balanus venustus* with *niveus*, *modestus* and *obscurus* as three of its subspecies, all with very similar and characteristically shaped terga with a short spur near the basi-scutal angle and hollowed out carinal half of the basal margin. Fourth and last *Balanus variegatus* is less easy to place, it differs from *B. amphitrite* in the teeth of the labrum and lacks the characteristic shape of tergum possessed by *B. venustus* and its subspecies. Darwin's var. *cirratus* I have treated as a variety of *B. variegatus* with beaded scuta, on the basis of Darwin's description, the type material is inadequate for a separation.

Concerning the characters used to separate the subspecies, the external colour pattern of the shell and the relationship of this pattern to the underlying shell structure are important. In some such as *B. amphitrite* the pores in the parietes lie underneath the coloured stripes on the outside and in others such as *B. venustus venustus* the pores are between the stripes. The radii are usually white but colour

or texture differences between the substance of the septa and the material filling the spaces between them is of interest especially when considered in relation to the colours seen on the surface or inside the substance of the parietes. There is a tendency for the colour opposite a septum of a parietal wall to be similar to the colour of the interseptal material of a radius (see Table I).

TABLE I.—*Colours Seen in Section of Parietes and Radii*

| | Parietes | | Radii | |
|---|---|---|---|---|
| Name | Opposite septa | Opposite Pores | Substance of septa | Substance filling interspaces |
| *amphitrite* | Off white | Dark slate with tinge of violet | Off white or with flecks of colour | Off white. |
| *venustus* | Purplish pink | White or slightly pinkish | Whitish | Purplish pink. |
| *pallidus* | White | White | Opaquely white | Hyaline white. |
| *stutsburi* | Upper part white, lower part mostly white | Upper part white, lower part purple pink | Opaquely white | Hyaline white. |
| *niveus* | Hyaline white | Opaque white | Opaquely white | Hyaline white. |
| *modestus* | Upper part white, lower part white or bluish-grey | Upper part white, lower part bluish-grey or reddish brown in section | Opaquely white | Hyaline white. |
| *obscurus* | Dark grey | Pale grey | White | Pale bluish-grey or reddish. |
| *variegatus* | Bluish-grey with white or cream flecks | Bluish-grey with purple flecks | Cream with a few purple flecks | Cream. |
| *cirratus* | Flecks of dirty pink | White | Not seen | Not seen. |

The pores themselves although very variable in most forms are very characteristic in *B. venustus obscurus*, where they are partially subdivided by a rib growing in from the outer lamina of the shell. The presence of subsidiary pores seems to be a feature of *B. pallidus* including its subspecies *stutsburi*.

The tergum is of greater diagnostic value than the scutum and the four species can usually be separated by its shape alone.

The labrum is very valuable for separating *B. amphitrite* from the rest ; but is of little further value.

The maxilla of *B. venustus venustus*, *B. venustus niveus* and *B. variegatus* tends to have the lower part of the inner edge slightly protuberant ; but this is a variable character and the lectotype of *B. venustus niveus* hardly shows it.

The only cirrus to provide useful characters is the third, which has curved hooks on the basal segments in *B. amphitrite*, *B. venustus niveus*, *B. v. obscurus* and to a lesser extent in *B. v. modestus*, these seem to be lacking in *B. venustus* s. str., *B. pallidus pallidus* and *B. pallidus stutsburi*.

The basal segments of the third cirrus of *B. pallidus pallidus* and *B. p. stutsburi* are short and broad and rather hairy compared with the others.

KEY TO DARWIN'S "VARIETIES"

1. Labrum with numerous teeth running down central notch. Shells with longitudinal purple-coloured stripes. Tergum with short spur and more than half its length distant from the basi-scutal angle . . . . . ***Balanus amphitrite***
Labrum with few teeth, usually none inside the groove . . . . . 2

2. Spur two or more times as long as broad. Scutum with triangular dark patch. Parietal walls with supplementary small pores outside the main pores ***Balanus pallidus*** 3

Tergum with short spur . . . . . 4

3. Shell white except for occasionally a pink edge to the compartments ***Balanus pallidus*** s. str.

Lower portion of shell purple upper part white . . ***Balanus pallidus stutsburi***

4. Tergum with spur less than half its length distant from the basi-scutal angle ***Balanus venustus*** 6

Tergum with a tapering spur over half its length distant from the basi-scutal angle. Shell with freckled stripes . . . . . ***Balanus variegatus*** 5

5. Scuta with lines of growth not beaded . . . . . ***Balanus variegatus*** s. str.

Scuta with beaded lines of growth (*fide* Darwin) . . ***Balanus variegatus cirratus***

6. Upper part of shell white, lower part uniform bluish-grey or with bluish-grey stripes corresponding with the pores in the wall of the shell . ***Balanus venustus modestus***

Shell with coloured or hyaline stripes corresponding with the septa between the pores 7

7. Stripes hyaline white . . . . . ***Balanus venustus niveus***

Stripes coloured . . . . . 8

8. Stripes purplish pink . . . . . ***Balanus venustus venustus***

Stripes narrow dark-grey more numerous near the base than higher up, parietal pores subdivided near to base . . . . . ***Balanus venustus obscurus***

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